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The functional morphology of *Hamites* and *Stomohamites* and the origins of the Turrilitidae

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KEY WORDS: Heteromorph ammonites, Anisoceratidae, Hamitidae, Turrilitidae, Phylogeny, Cladistics, Functional Morphology, Cretaceous.

ABSTRACT: Cladistic analysis of the heteromorph ammonites of the Albian (Lower Cretaceous) indicates that the Turrilitidae, exclusive of the genus *Pseudhelicoceras*, is monophyletic and derived from the Hamitidae. The ancestral hamitids developed helical coiling during the early stages of ontogeny to allow for the subsequent re-folding of the shell into the adult hook-shaped living chamber. Progenetic derivatives of these hamitids had progressively more truncated adult hooks, finally losing the hook part of the living chamber altogether, giving rise to the completely helical primitive turrilitids such as *Proturrilitoides*. Comparisons of the phylogeny with the functional motphology of the species analysed indicates a progressive shift occurred between the benthonic hamitids and the planktonic turrilitids.

RIASSUNTO: Un'analisi cladistica delle ammoniti eteromorfe dell'Albiano (Cretaceo inferiore) indica che le Turrilitidae, dalle quali viene escluso il genere *Pseudhelicoceras*, rappresentano un gruppo monofiletico derivante dalle Hamitidae. Le hamitidi ancestrali svilupparono un avvolgimento elicoidale durante gli stadi iniziali della loro ontogenesi per consentire un successivo ripiegamento della conchiglia risultante nella forma ad uncino della camera d'abitazione dell'adulto. Senza la fase elicoidale, gli stadi di sviluppo successivi della camera d'abitazione sarebbero risultati piú limitati nel dispiegamento delle possibili morfologie acquisite. Discendenti progenetici di queste hamitidi possedettero allo stadio adulto forme ad uncino progressivamente piú troncate, e successivamente persero del tutto la parte ad uncino della camera d'abitazione, dando cosí origine a turrilitidi primitive dalla forma completamente elicoidale, come ad esempio *Proturrilitoides*. La morfologia della linea di sutura con ampi lobi era simile in queste turrilitidi primitive e nelle hamitidi; del tutto simile risultava essere anche l'ornamentazione delle conchiglie, caratterizzata da coste semplici e da aperture ristrette. In alcune di queste turrilitidi, si sviluppó una serie di tubercoli ad orientamento asimmetrico lungo il fianco esterno della spirale della conchiglia. Sebbene si pensi sovente al genere *Pseudhelicoceras* come ad un rappresentante primitivo di queste turrilitidi tubercolate, in effetti si puó mostrare attraverso un'analisi cladistica che esso é piú strettamente imparentato alle Anisoceratidae e alle Nostoceratidae, in cui le linee di sutura possiedono stretti lobi laterali e umbilicali, varici spaziate a intervalli regolari e spine appaiate simmetricamente da un lato e dall'altro del sifuncolo. Un esame comparato dei risultati ottenuti dalla filogenesi e dalla morfologia funzionale delle specie analizzate indica una progressiva modificazione adattativa che portó al passaggio dalle hamitidi bentoniche alle turrilitidi plantoniche. Le hamitidi possiedono conchiglie allungate a strettamente ripiegate; quando l'animale estendeva il corpo, questo tipo di conchiglia permetteva all'apertura di essere orientata in avanti e leggermente verso il basso in direzione del fondale marino. Queste ammoniti erano probabilmente in grado di muoversi sul fondale adoperando i loro tentacoli in maniera simile a quella di un polpo moderno. Quando l'animale aveva esigenza di ritirarsi all'interno della conchiglia, quest'ultima probabilmente si sollevava dal fondale marino, il che rendeva l'animale meno suscettibile di attacco da parte di predatori bentonici come ad esempio i granchi, che sembra abbiano predato queste ammoniti. Le turrilitidi hanno un orientamento fisso, con l'apertura diretta quasi esattamente verso il basso. Questo orientamento limiterebbe le capacitá dell'animale di nuotare orizzontalmente, ma consentirebbe ad esso di spostarsi verticalmente in alto ed in basso nella colonna d'acqua. In questo, le turrilitidi rassomiglierebbero ai moderni calamari della famiglia Cranchidae, reperibili in gran numero in ambienti neritici dove si nutrono di plancton e piccoli pesci. Puó darsi che gli stadi precoci elicoidali delle hamitidi siano stati caratterizzati da simili adattamenti ecologici, seguiti da uno stile di vita bentonico una volta raggiunta la maturitá; in tal caso, si possono interpretare le turrilitidi elicoidali come ammoniti che hanno mantenuto da adulte adattamenti ecologici che caratterizzarono gli stadi giovanili dei loro antenati. La medesima condizione elicoidale venne acquisita da quelle hamitidi che possedevano conchiglie hamiticoniche strettamente ripiegate. Tale condizione consentiva alla seconda porzione diritta della conchiglia di svilupparsi al di sotto e ben oltre la spira iniziale; tale modalitá di crescita non si sarebbe potuta realizzare nel caso in cui la spira iniziale fosse risultata appiattita e giacente nel medesimo piano delle porzioni diritte della conchiglia.

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INTRODUCTION

The Turrilitidae are a group of helically coiled ammonites that appeared during the Middle Albian and persisted into the Upper Cenomanian . The group is supposedly polyphyletic, having been derived partly from the Hamitidae and partly from the Anisoceratidae (MATSUMOTO, 1967; WRIGHT *et al*, 1996). This hypothesis is based upon the differences in morphology of two earliest known turrilitids, *Proturrilitoides* BREISTROFFER, 1940 and *Pseudhelicoceras* SPATH, 1921, which appeared during the Middle Albian. *Proturrilitoides* consists of an open, regularly helical shell with simple annular ribs and in some species at least paired collars around an apertural constriction. Simple ribs and apertural modifications such as these are common among many of the Hamitidae. In contrast to *Proturrilitoides*, the helix of *Pseudhelicoceras* is rather less regular, becoming distinctly more open in the later stages of ontogeny. In addition, the ornamentation consists of ribs which bifurcate between paired spines. There is one pair running along either side of the siphuncle, and a second with a spine over each lateral lobe. This style of ornament is very similar to that of *Anisoceras* PICTET, 1854, which while the body chamber consists of a planar hook, is helically coiled initially. Consequently, it has been argued by KLINGER & KENNEDY (1978) that both *Proturrilitoides* and *Pseudhelicoceras* are "neotenous offshoots" of the Hamitidae and the Anisoceratidae respectively, and that through the Albian these two lineages gave rise non-spine bearing turrilitids like *Turrilitoides* SPATH, 1923 on the one hand and the spine bearing turrilitids such as *Paraturrilites* BREISTROFFER, 1947 on the other.

PHYLOGENY

I have elsewhere described a phylogenetic analysis of the Albian heteromorph ammonites using computer-based parsimony techniques (MONKS, 1999); and the techniques used therein need not be repeated here in detail. Essentially a range of character suites were identified as having potential value in ammonite systematics; these included the position of the siphuncle, the shape of the suture line, degrees of helicosity, and the ornamentation of the shell. The resulting cladogram is given in Fig. 1. From this analysis it is evident that *Pseudhelicoceras* is derived from the Anisoceratidae, but is not ancestral to the spine bearing turrilitids, which are closer to *Proturrilitoides* and *Turrilitoides*, and evolved spines independently as had previously been thought. *Pseudhelicoceras* shares a similar sutural morphology with *Anisoceras*, with narrow-stemmed bifid lateral and umbilical lobes. In contrast, the suture lines of the other *Proturrilitoides* and *Paraturrilites* resemble one another more closely, with rather broad lobes; and in addition unlike *Pseudhelicoceras* all four lobes of the suture line are distinctly asymmetrical. Another difference is the evident with respect to the spines of *Pseudhelicoceras* and *Paraturrilites*. As noted above, the spines of *Pseudhelicoceras* and *Anisoceras* are virtually identical both in distribution and relatationship with the ribs. With *Paraturrilites* and the other spine bearing turrilitids, the spines are not paired, but develop on the outer flank of the coil only, and there is no looping of the ribs between the spines. Therefore the analysis supports the view of SCHOLZ (1979) that *Pseudhelicoceras* should be excluded from the Turrilitidae and instead included with the Anisoceratidae. The remaining Albian turrilitids form a monophyletic group, the sister groups of which includes the Upper Albian hamitids usually referred to the genus *Stomohamites* BREISTROFFER, 1940. The most basal species, *Stomohamites virgulatus* BROGNIART, 1822, has a loosely coiled horseshoe-shaped shell with no trace of helicosity (Fig. 2). Closer to the Turrilitidae is *Stomohamites parkinsoni* (FLEMING, 1814), which is helically coiled through the juvenile stage but yields to planar coiling at maturity in the form of a hook-shaped body chamber. *Stomohamites parkinsoni* itself probably includes a complex of species (see discussions by SPATH, 1941, SCHOLZ, 1979 and MONKS (1998). All are very similar in ornamentation and suture-line morphology, but vary considerably in coiling mode. Most of them have a relatively brief helical stage, followed by either two or three sub-parallel shafts connected by tight bends (Fig. 3). In others, such as *Stomohamites ibex* SPATH, 1941, the helical stage is larger and consists of more rotations, and the planar section is a brief, U-shaped hook (Fig. 4). The suture line, ribbing, and apertural modifications of these helically coiled hamitids are essentially similar to the early turrilitids; the key difference is therefore the complete loss of the planar, hook-shaped body chamber.

It is critical to understand that *Stomohamites virgulatus* may not have given rise to *Stomohamites parkinsoni* and that species in turn to the Turrilitidae. The cladogram indicates only that these species are progressively more closely related to the Turrilitidae, and not ancestors italicize. This is especially important when it is noted that *Stomohamites* appears later in the fossil record (during the Upper Albian) than *Proturrilitoides* (Middle Albian). The inadequacies of the fossil record have been widely discussed, and need not be commented on here (see Smith, 1993); but it is still probably safer to regard these *Stomohamites* species as morphologically similar, but not identical with, the postulated ancestors of the Turrilitidae.

The remainder of this paper accepts that the evolution of the Turrilitidae from the Hamitidae broadly followed a pattern consistent with the cladogram described above. The evolution of the Turrilitidae can be described as having occurred in a two steps. First was the acquisition of helical coiling within the Hamitidae, which was initially a feature of the juvenile phase. This was followed by the prolongation of the helix throughout ontogeny and the loss of the planar hook-shaped living chamber. This latter process is essentially paedomorphic in nature, consisting of both neotenous and progenetic elements (MCNAMARA, 1990). On the one hand the increase in size of the helically coiled section was achieved by delaying the point at which the ammonite shifted from helical to planar growth; and on the other hand the reduction in the size of the hook-shaped living chamber required a premature completion of the adult part of the shell. This is summarized in Fig. 5. The remaining question is therefore why did the hamitids evolve helical coiling at all?

FUNCTIONAL MORPHOLOGY

The functional morphology of heteromorph ammonites such as the hamitids has been widely discussed with varying conclusions. While some have considered the open coiling and poor streamlining of the shell to be indicative of a drifting, passive mode of life in the plankton (WESTERMANN, 1996), others have viewed them more as benthic, octopus-like crawlers for exactly the same reasons (EBEL, 1992). One persistent belief is that the body occupied the entire living chamber. If this is the case, then ammonites with hook-shaped living chambers are usually oriented with the aperture upwards, and away from the sea floor (Fig. 6a). Because the uncoiled nature of the shell would separate the centres of mass and buoyancy, these ammonites would have been very stable, making it difficult for the animal to alter the orientation of the shell (TRUEMAN, 1941). Such animals would have been unable to have gathered food from the sea floor. This has been taken to support the planktonic mode of life hypothesis. However, MONKS & YOUNG (1998) disputed the assumption that heteromorph ammonites completely occupied their living chambers. If the soft body parts occupied only part of the shell, then orientation would depend upon the position of body within the shell, i.e., whether the body was extended or withdrawn (Figs. 6b, c). A key implication of such a model is that some uncoiled ammonites which had been thought of as planktonic could have been benthic, since the aperture could have been oriented with the aperture toward the sea floor.

One pattern observed by MONKS & YOUNG (1998) is that hamiticonic ammonites have the greatest angles of rotation caused by pulling the body back and forth within the living chamber (and perhaps best able to orient the body toward the sea floor?). Such shell shapes are also relatively elongate and streamlined along this axis, and the body chamber is very straight. A rapid contraction of the retractor muscles could have expelled a powerful stream of water directed along the long axis of the shell, perhaps useful in escaping from predators (Fig. 7). Among *Hamites* and *Stomohamites*, those forms which are hamiticonic also have helical juvenile stages. The ontogeny of these shells shows clearly that the helix is essential to allow the second straight shaft to grow underneath and beyond the initial coil. Without such helicosity, the second straight shaft coil would have eventually impacted with the initial coil, and the second hook and third straight shaft could never have developed. Therefore, it is likely that helicosity evolved primarily to allow complete development of an hamiticonic adult shell.

Helical shells behave in a different way to the planar spiral shells of typical ammonites. Regardless of the size of the body within the living chamber, they tend to orient themselves with the apex pointing upwards and the aperture toward the sea floor. As KLINGER (1980) and WARD (1986) have discussed, helical shells may be most useful to ammonites which are vertical migrators. The reasons for this include the relatively good streamlining of the shell in the vertical plane (with the point of the apex leading) and the orientation of the exhalent current, assuming they swam with jet propulsion, along the long axis of the animal. KLINGER (1980) has further suggested that the apical displacement of the siphuncle characteristic of the Turrilitidae may be an additional adaptation to such a lifestyle, allowing more efficient emptying of the chambers of the phragmocone.

DISCUSSION

It is argued here that helical coiling evolved to allow for the hamiticonic shell morphology which was well suited to a benthonic lifestyle. MONKS & YOUNG (1998) suggested that such an octopus-like lifestyle fits well with the distribution of these unusual ammonites. MARCINOWSKI & WIEDMANN (1990) have commented on their preference for clay or marly facies rather and BATT (1989) has noted that hamiticonic ammonites are absent from anoxic bottom water sediments even when the upper waters were perfectly well oxygenated. Additional evidence in support of this theory may come from sublethal damage found on many specimens of *Hamites* from the Gault Clay at Folkestone, in Southern England. An example is shown in Fig. 8 of *Hamites intermedius* SOWERBY, 1814. The shell has been pee-

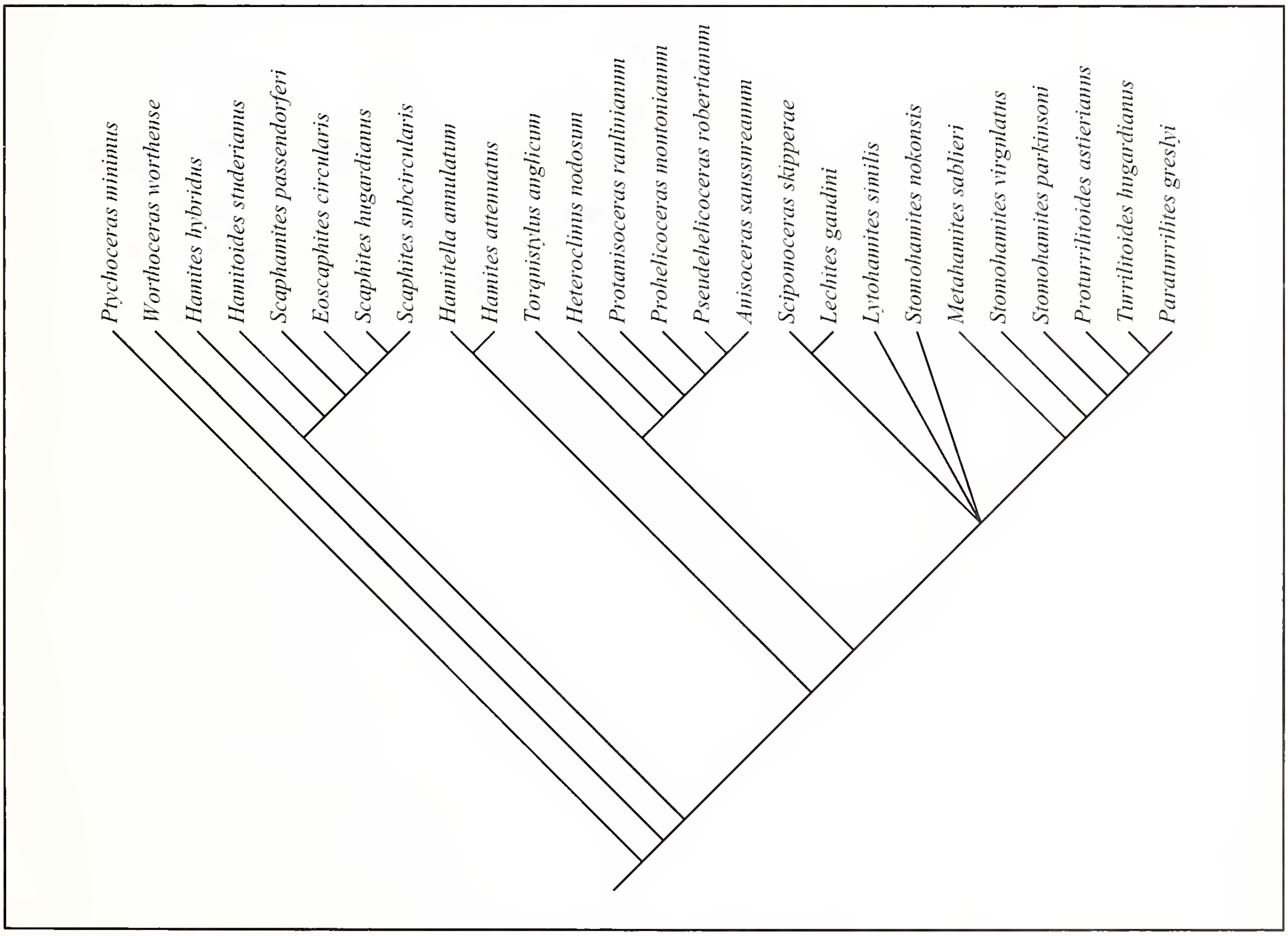

Fig. 1: Cladogram of the Albian heteromorph ammonites based on Monks (1999).

led back from the aperture and then repaired. Such damage is typically seen in snails which have been attacked by peeling predators such as crabs, which are almost exclusively benthic and are known to have been radiating during the Cretaceous (Vermeij, 1977).

However, it would appear that helical coiling also benefited the juvenile ammonite, perhaps by increasing its efficiency as a vertically-migrating plankton feeder. Cladistic analyses support the hypothesis that progressive reduction in the development of the adult hook-shaped living chamber took place within one clade, ultimately giving rise to the completely helical Turrilitidae. This particular branch of the cladogram is therefore congruent with a paedomorphocline (*sensu* McNamara, 1997). Presumably this new mode of life was a successful one, and allowed these ammonites to occupy new ecological niches. Between the planar and the only briefly helical ancestral hamitids and the completely helical *Proturrilitoides*, there was a series of intermediates spending progressively more time in midwater and less time on the sea floor.

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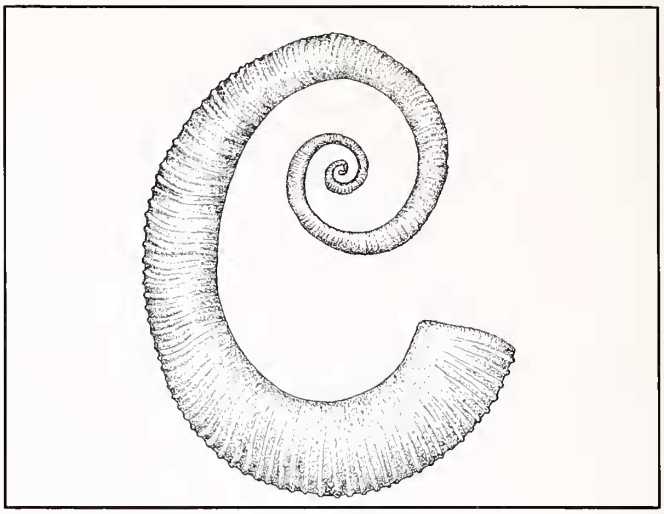

Fig. 2: Reconstruction of the complete shell of *Stomohamites virgulatus*.

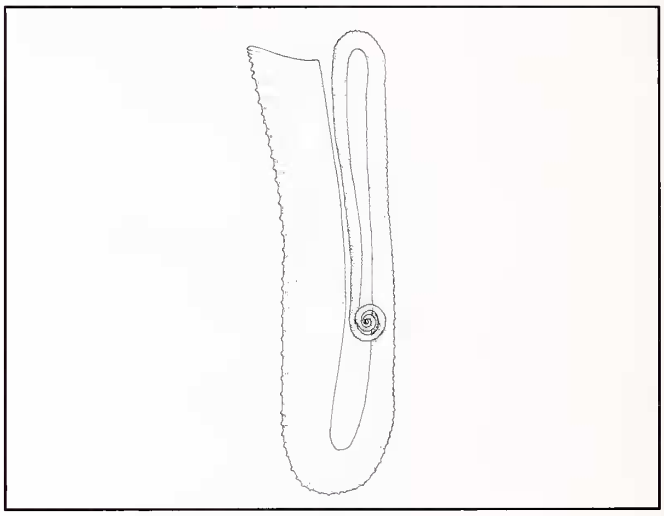

Fig. 3: Reconstruction of *Stomohamites parkinsoni*.

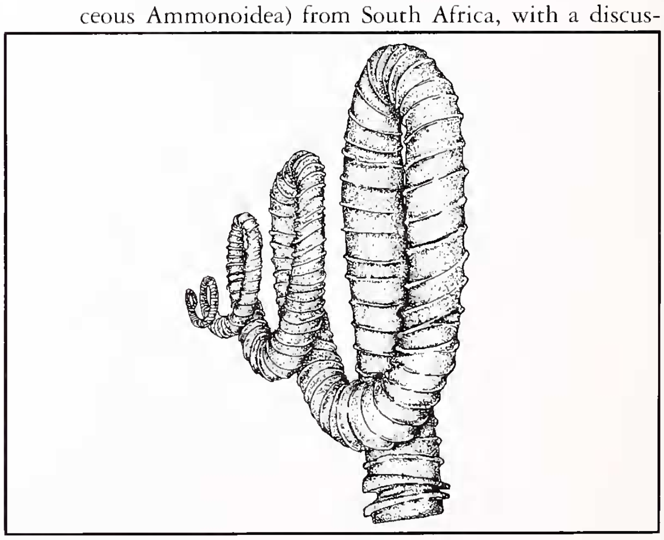

Fig. 4: Reconstruction of *Stomohamites ibex*.

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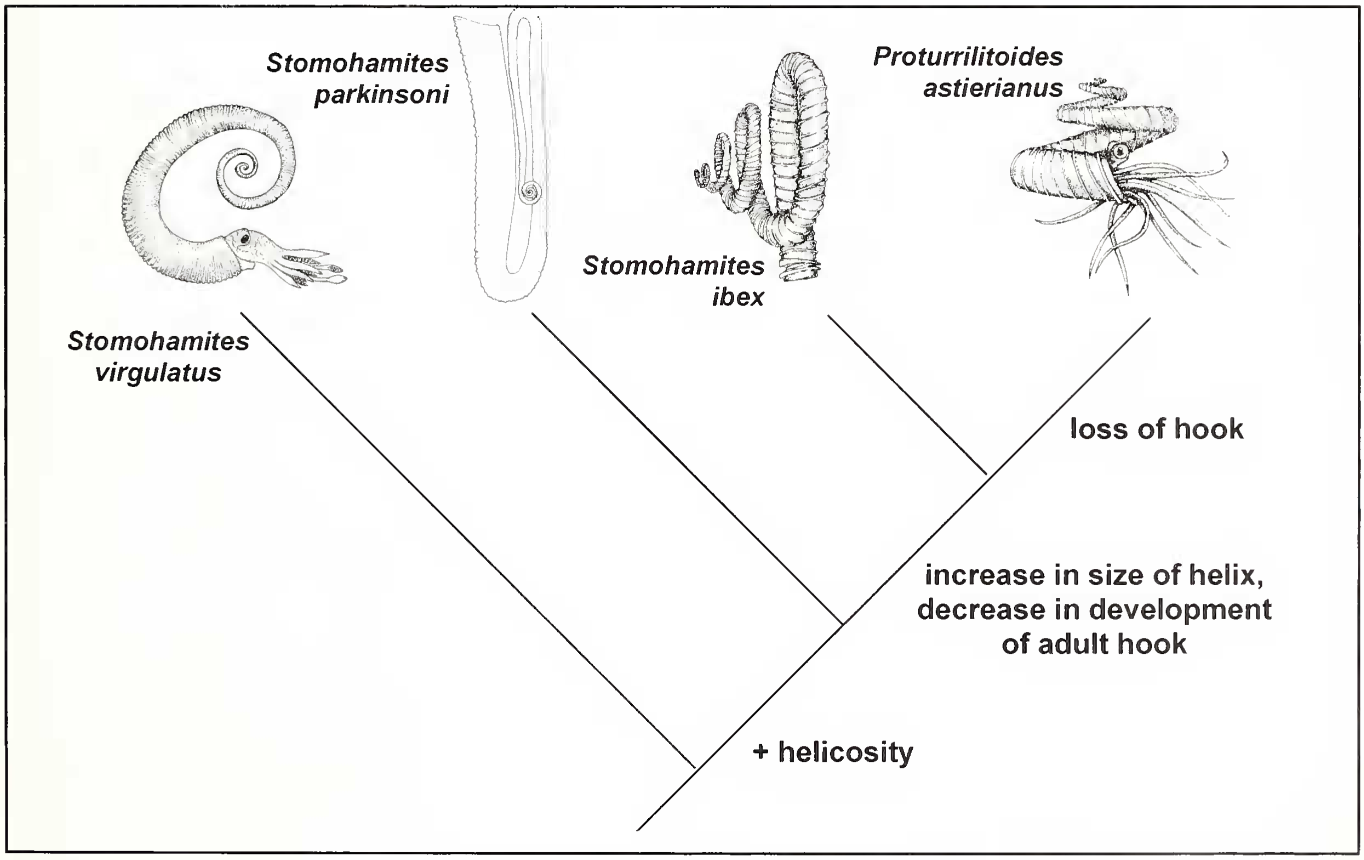

Fig. 5: Cladogram of the relations of the primitive turrilitid *Proturrilitoides astierianus* and its immediate sister taxa within the hamitids, *Stomohamites ibex*, *St. parkinsoni*, and *St. virgulatus*. Progressive expansion of the helical stage and reduction in the development of the adult hook are likely to have been heterochronic processes.

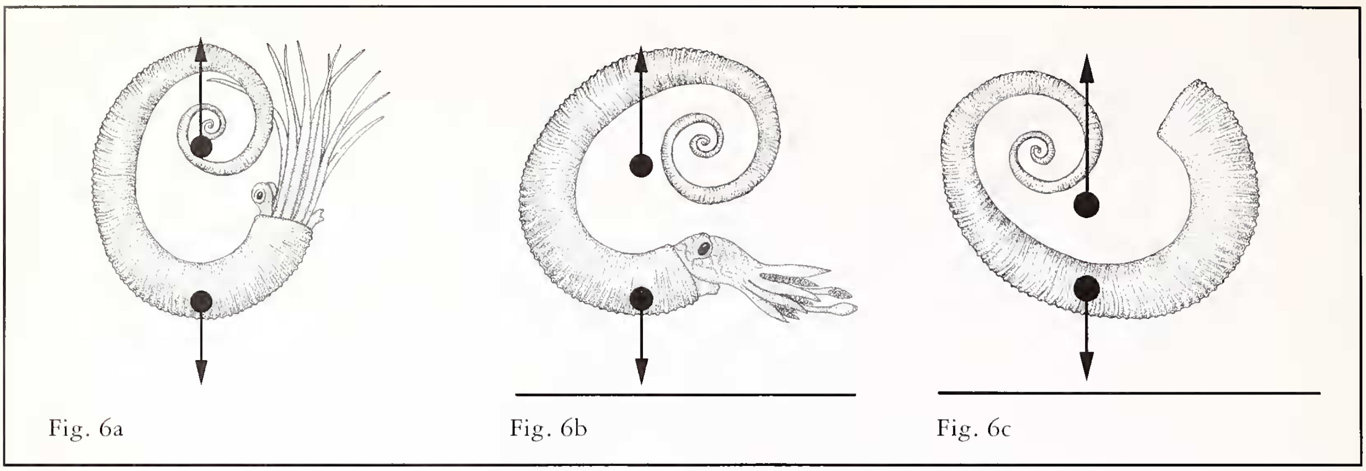

Fig. 6a: TRUEMAN (1941) considered open coiled heteromorph ammonites such as *Stomohamites virgulatus* to have had upward oriented apertures based upon the position of the centre of mass (downwards arrow) and centre of buoyancy (upwards arrow). This is based on the assumption that the soft body parts of the animal completely filled the living chamber. Fig. 6b: Monks & Young (1998) suggested that the body may not have completely filled the living chamber, resulting in the centre of mass being located close to the aperture when the head and arms ere extended such as when feeding. In this case, the ammonite would have been oriented with the aperture close to the sea floor. Fig. 6c: According to the model proposed by Monks & Young (1998), retraction of the body into the shell would have caused the shell to rotate away from the sea floor as the centre of mass moved towards the back of the shell.

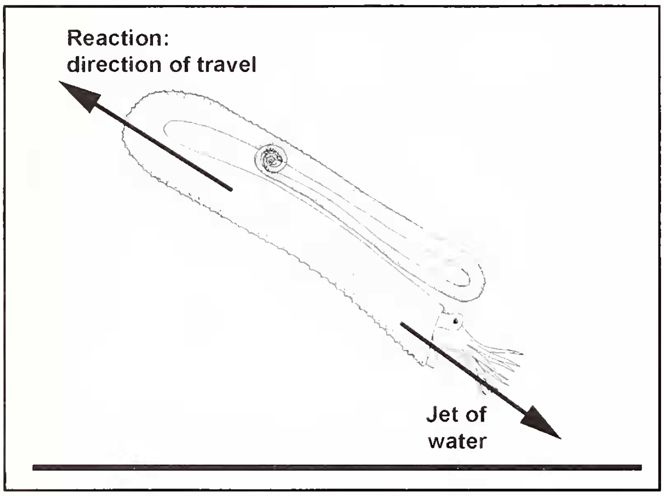

Fig. 7: The tight folding of some heteromorphs may have streamlined the shell in the direction of the escape reaction. By pulling the body into the long, straight living chamber, a powerful jet of water could have propelled the ammonite way from danger.

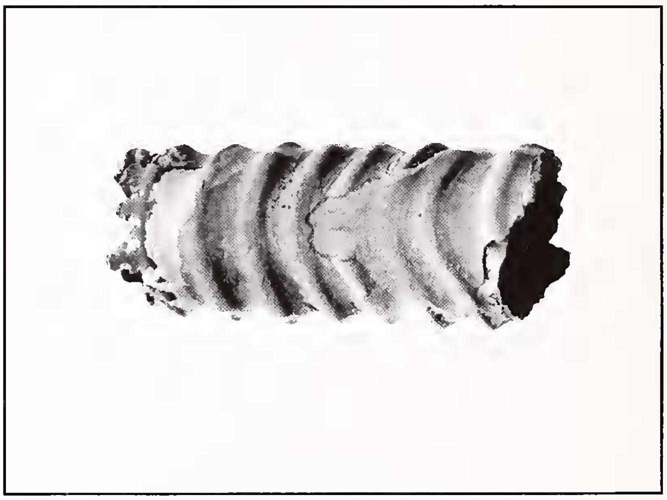

Fig. 8: Damage probably caused by a peeling predator such as a crab upon an Upper Albian hamitid from the Gault Clay of Folkestone, Kent, UK. The shell was peeled from the aperture (downwards), consistent with such predation on snails in modern times. Subsequent repair indicates that this was not post mortem damage.

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